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LETTER

Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice

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Abstract

Apex predators such as large carnivores can have cascading, landscape-scale impacts across wildlife communities, which could result largely from the fear they inspire, although this has yet to be experimentally demonstrated. Humans have supplanted large carnivores as apex predators in many systems, and similarly pervasive impacts may now result from fear of the human 'super predator'. We conducted a landscape-scale playback experiment demonstrating that the sound of humans speaking generates a landscape of fear with pervasive effects across wildlife communities. Large carnivores avoided human voices and moved more cautiously when hearing humans, while medium-sized carnivores became more elusive and reduced foraging. Small mammals evidently benefited, increasing habitat use and foraging. Thus, just the sound of a predator can have landscape-scale effects at multiple trophic levels. Our results indicate that many of the globally observed impacts on wildlife attributed to anthropogenic activity may be explained by fear of humans.

Keywords

Ecology of fear, human impacts, landscape of fear, large-scale field manipulation, playback experiment.

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INTRODUCTION

The fear of predators can itself be powerful enough to drive demographic and community-level changes in wildlife systems, as demonstrated in a growing number of recent experiments (Zanette *et al*. 2011; LaManna & Martin 2016; Suraci *et al*. 2016). The impacts of fear are typically mediated by changes in prey behaviour (Schmitz *et al*. 1997; Brown & Kotler 2004), which may vary spatially with changes in the prey's perception of predation risk across the landscape (Gaynor *et al*. 2019). Anthropogenic activity is reshaping wildlife behaviour across human-dominated landscapes, disrupting movement (Tucker *et al*. 2018), forcing shifts to nocturnality (Gaynor *et al*. 2018) and changing the way predators interact with their prey (Smith *et al*. 2015). Humans are themselves major predators (Darimont *et al*. 2009), killing some species, particularly large and medium-sized carnivores, at many times the rate at which they are killed by non-human predators (Darimont *et al*. 2015), and fear of the human 'super predator' (Darimont *et al*. 2015) may therefore be a significant driver of observed changes in wildlife behaviour (Oriol-Cotterill *et al*. 2015; Suraci *et al*. 2019). Given that humans have evidently superseded large carnivores as apex predators in many ecosystems (Ordiz *et al*. 2013a; Oriol-Cotterill *et al*. 2015; Kuijper *et al*. 2016), our mere presence may be expected to generate landscapes of fear (Gaynor *et al*. 2019) with spatial extents and breadth of trophic impacts equal to or greater than those presently attributed to large carnivores (Laundré *et al*. 2001; Palmer *et al*. 2017). Yet, whether fear of the human 'super predator', or indeed any large apex predator, generates landscapes of fear with impacts across wildlife communities remains to be tested experimentally.

A large number of correlative studies suggest that some wildlife species respond fearfully to human activity (Fernandez-Juricic *et al*. 2005; Stankowich & Blumstein 2005; Bateman & Fleming 2017), but whether such responses are driven by perceived risk from humans as predators or by a generalised response to 'disturbance' (e.g. sudden noises, looming objects) is often unclear (Frid & Dill 2002; Stankowich 2008). Experimentally testing predator-specific responses requires manipulating something the prey is likely to perceive as being specific to that predator (e.g. vocalisations, odours) in conjunction with a non-predator-specific control for the generalised disturbance potentially caused by manipulations. Recently, small-scale (≤ 50 m), short-term (≤ 2 h) controlled experiments on single prey species have demonstrated that wildlife regularly killed by humans exhibit strong fear responses to human vocalisations, just as prey respond fearfully to the vocalisations of any other predator (Hettena *et al*. 2014; McComb *et al*. 2014; Clinchy *et al*. 2016; Smith *et al*. 2017). By isolating human predator-specific responses, such experiments differentiate the impacts of fear of humans as predators from the myriad other aspects of the anthropogenic environment likely to affect wildlife behaviour [e.g. enhanced food resources, habitat fragmentation (Bateman & Fleming 2012; Newsome *et al*. 2015; Tucker *et al*. 2018)]. By scaling up such experiments, we can thus quantify how the fear of humans as predators impacts wildlife at the landscape and community levels.

To experimentally test whether the magnitude of effects caused by fear of an apex predator (in this case humans) can extend to having landscape-scale impacts across wildlife communities, we conducted spatially replicated, landscape-scale manipulations of perceived human presence. We sequentially

broadcast playbacks of people talking or control sounds for 5 weeks (followed by the opposite treatment for a subsequent 5 weeks) over spatial scales (1 km^2) comparable to those of the largest mammalian predator exclusion experiments (Salo *et al*. 2010), and simultaneously quantified the responses of multiple mammal species across three trophic levels. The study was conducted in the Santa Cruz Mountains of central California. Like an increasingly large proportion of the planet (Venter *et al*. 2016), this region consists of wildlife habitat in close proximity to urban and suburban development, and is thus heavily used by people (Wang *et al*. 2015). The Santa Cruz Mountains support a single native large carnivore, the mountain lion (*Puma concolor*), and several smaller predators (for brevity, referred to as 'medium-sized carnivores') including bobcats (*Lynx rufus*), striped skunks (*Mephitis mephitis*) and Virginia opossums (*Didelphis virginiana*), all of which have been shown to alter their behaviour in response to the gradient of human development that exists across the region (Wilmers *et al*. 2013; Wang *et al*. 2015). Small-scale experiments replicated across this region previously demonstrated that mountain lions here exhibit strong fear responses to hearing human voices, fleeing food caches and feeding less as a consequence (Smith *et al*. 2017). Medium-sized carnivores similarly exhibited fear-induced reductions in feeding and shifts in temporal activity in response to the small-scale experimental presentation of human voices (Clinchy *et al*. 2016). As is true for large and medium-sized carnivores globally (Ordiz *et al*. 2013a; Darimont *et al*. 2015), humans are a major source of mortality for mountain lions in our study area, with legal and illegal shooting accounting for 59.1% of known-cause mortalities of collared animals since 2008 (C. Wilmers, *unpublished data*). Bobcats, skunks and opossums are all common targets of predator control (Conner & Morris 2015), and are all legally hunted in California, with no legal limits on killing skunks and opossums (California Department of Fish & Wildlife 2018). Correlational results from our study area indicate that bobcats are sensitive to risk from humans, decreasing diurnal activity in areas of high human development, but suggest that skunks and opossums may prefer more developed areas (Wang *et al*. 2015). Medium-sized carnivores such as skunks and opossums often rely heavily on human subsidies, including food waste (Bateman & Fleming 2012), and thus could be forced to balance the risk of anthropogenic mortality against the benefits of living near humans.

Given the evidence that carnivores fear humans as predators, both in our study area and in general, our objective was to experimentally test whether such fear leads to landscape-scale impacts across wildlife communities. We quantified the large-scale effects of fear of humans as predators on carnivore movement, activity and foraging behaviour using GPS collars (mountain lions) and camera traps (bobcats, skunks and opossums). Correlational studies suggest that fear-induced suppression of carnivore behaviour by apex predators may cascade to benefit small mammal prey (Brook *et al*. 2012; Gordon *et al*. 2015), although this has yet to be shown experimentally. We therefore additionally tested whether the fear that humans induce in carnivores can have cascading effects on the behaviour of lower trophic level animals, using live trapping and provisioned food patches to document effects on habitat use and foraging by small mammals (deer mice *Peromyscus* spp. and woodrats *Neotoma fuscipes*) known to be preyed upon by several of the carnivores in our study (Azevedo *et al*. 2006; Smith *et al*. 2018).

In a major reclarification of the landscape of fear concept, Gaynor *et al*. (2019) define it as spatial variation in the prey's perception of predation risk, influenced by, but distinct from, both the physical landscape and actual risk of mortality from predators. Here, we use the sequential presentation of human and control vocalisations at each of our 1-km^2 sites to manipulate the perception of predation risk across the same physical landscapes, thus keeping physical characteristics and actual mortality risk constant. We thereby experimentally demonstrate that a landscape of fear, resulting solely from variation in the perception of risk from an apex predator, can have pervasive effects across wildlife communities. That such effects can result from the fear of humans as predators indicates that this may be an important factor underlying many of the globally observed changes in wildlife behaviour associated with anthropogenic activity (Gaynor *et al*. 2018; Tucker *et al*. 2018).

METHODS

Study area

The study was conducted at two 1-km^2 experimental sites (SA and SVR), separated by 26 km (Fig. S1). Both sites were closed to public access, and human presence was therefore low relative to elsewhere in the Santa Cruz Mountains. The presence of humans (including researchers) and vehicles did not differ between experimental sites during the study (Mann–Whitney *U*-test comparing occurrences per camera night on $n = 12$ cameras per site; humans: $P = 0.643$; vehicles: $P = 0.655$). Work was conducted between 29 May and 31 August 2017.

For additional details on the study area and species, see Appendix S1. All procedures described below were approved by the Institutional Animal Care and Use Committee of the University of California, Santa Cruz (Protocol WilmC1612) and the California Department of Fish and Wildlife (Permits SC-11968 and SC-12383).

Playbacks and study design

We manipulated the perceived presence of humans on the landscape using playbacks of human and control vocalisations broadcast sequentially for 5 weeks each at both 1-km^2 experimental sites. Following established protocols (Suraci *et al*. 2016; Smith *et al*. 2017), we compared wildlife responses to human vocalisations with responses to Pacific treefrog (*Pseudacris regilla*) vocalisations. Tree frogs, like humans, can be heard both day and night in our study area, but unlike humans, their perceived presence should be completely benign given that treefrogs are unlikely to be predators, competitors or prey of any study species. As discussed in detail in Appendix S1 (Supplementary Methods – Playback Treatments), there is ample evidence to suggest that wildlife in the

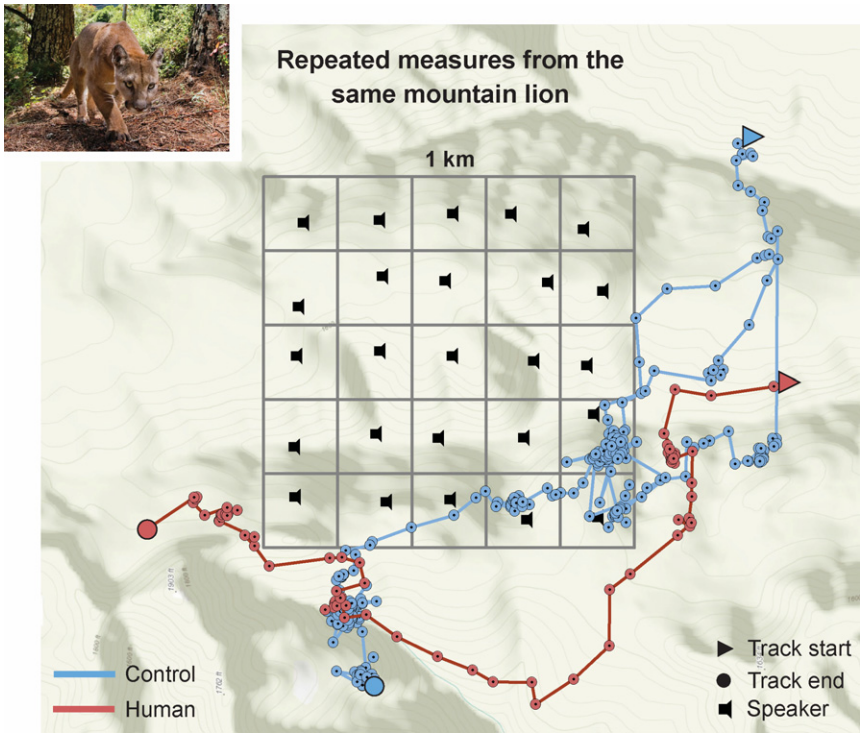

Figure 1 Example of the landscape-scale impacts of fear of humans on mountain lion behaviour, illustrated by repeated-measures movement tracks from a single mountain lion during the control (blue) and human (red) treatments. Points are 5-min GPS fixes, and connecting lines illustrate the approximate movement path. Black speaker icons denote playback speaker locations and the grey grid illustrates the 1-km^2 experimental site. Photo © Sebastian Kennerknecht.

Santa Cruz Mountains will be familiar with both human and tree frog vocalisations.

Playbacks were broadcast from 25 speakers arranged in a 5 × 5 grid at each experimental site (Fig. S1). Each speaker played a randomised playlist of human or frog recordings (n = 10 exemplars of each) interspersed by silence such that each individual speaker was broadcasting 40% of the time and silent 60% of the time. Speakers were thus continuously active, but presentation of cues was random and sporadic across the playback grid. The human treatment thereby mimicked a wildland–urban interface in that human vocalisations were relatively infrequent, but from any location within the playback grid, a human could occasionally be heard at any time. All playbacks were broadcast at a standardised volume of ~ 80 dB at 1 m (human = 78.7 dB ± 1.9 SD; frog = 79.2 dB ± 2.4). Additional details of the playback treatments are provided in Appendix S1.

We employed a repeated-measures design with each experimental site receiving either the human or control treatment for 5 weeks (treatment period 1), followed by the opposite treatment for a subsequent 5 weeks (treatment period 2) with 8 days of silence between the two treatment periods. Thus, both experimental sites received each treatment in opposite order, and as such, detecting consistent responses to playback treatments across sites is critical to concluding that treatments had a significant effect. We therefore included a test for treatment × site interaction in all analyses presented below and only concluded that treatments drove observed changes when no significant interaction was detected (see Tables S1–S8). We also present visualisations of site-level data for all analyses (Figs S2–S7) to illustrate the consistency of treatment effects across sites.

Monitoring mountain lion responses to playbacks

We monitored the responses of seven mountain lions (four females and three males) whose home ranges overlapped one of our two experimental sites. Five individuals (four females and one male) used SVR, while two males used SA. Mountain lions were captured using trailing hounds or cage traps and fitted with GPS collars (GPS Plus, Vectronics Aerospace, Berlin, Germany) with a 5-min fix interval.

We focused mountain lion movement analyses on only those periods when an individual was within audible range of a playback grid (termed an 'encounter' with the playbacks) and used a repeated-measures design to compare responses of individual mountain lions to both playback treatments (Fig. 1). We considered the audible range of the speakers to extend 200 m out from the speaker grid itself (see Appendix S1), and also ran all analyses using a smaller buffer size (150 m), which yielded similar results. Five mountain lions encountered the playbacks on multiple occasions, with subsequent encounters separated by 19.1 days on average (range = 4.6–38.6 days). The median number of encounters per individual was 2 (range = 1–5; total encounters across all individuals = 17).

For all mountain lion GPS locations taken within the 200 m audible range, we determined the distance to the

nearest playback speaker and the animal's movement speed. For each encounter, we then calculated average distance to the nearest speaker (an estimate of speaker avoidance) and average movement speed across all locations for that encounter. We took the inverse of movement speed as an estimate of 'cautiousness', moving more slowly being considered greater cautiousness. We tested for effects of playback treatment, experimental site and a treatment × site interaction on avoidance and cautiousness using linear mixed-effects models (LMM), with mountain lion ID as a random effect. Cautiousness (movement speed^{-1}) was log-transformed to meet normality assumptions. Unless otherwise noted, we confirmed adequate fit of these and all other frequentist models through visual inspection of residuals and assessed significance of model terms using Type II Wald's chi-squared tests (Table S1). Finally, we confirmed that observed changes in medium-sized carnivore behaviour between treatments (see below) were not due to changes in mountain lion presence by testing for differences in time spent by mountain lions near experimental sites (see Appendix S1 and Table S1 for details).

Medium-sized carnivore responses to playbacks

At each experimental site, we deployed a grid of 12 camera traps, which ran continuously throughout the experiment (camera deployment details in Appendix S1). We scored camera trap images for the presence of three medium-sized carnivore species that occurred at both experimental sites, which prior correlational research in the region indicates are affected by human development (Wang *et al*. 2015): bobcats, striped skunks and Virginia opossums. We considered images of the same species on the same camera to be separate detections if they were separated by > 30 min (Wang *et al*. 2015; Suraci *et al*. 2017). Two other medium-sized carnivore species (raccoons *Procyon lotor* and gray foxes *Urocyon cinereoargenteus*) occasionally occurred on camera traps, but were detected too infrequently to permit statistical analyses, raccoons only occurring on three cameras at one site and foxes only during a subset of treatment periods.

Bobcat temporal activity

Prior research (Wang *et al*. 2015) shows that, whereas bobcats are diurnally active 29.6% of the time, skunks and opossums are almost exclusively nocturnal (94 and 96.6% nocturnality respectively). We therefore tested whether playback treatments affected temporal activity for bobcats, the only species with sufficient diurnal activity to expect an effect. We calculated the overlap between temporal activity during control and human treatments using the kernel density estimation procedure described by Ridout and Linkie (Ridout & Linkie 2009; Linkie & Ridout 2011). We estimated probability density distributions for bobcat occurrences on camera across the 24-h day separately for the control and human treatment periods. We then calculated the coefficient of overlap ($\hat{\Delta}$, range 0–1) between these two activity distributions (Ridout & Linkie 2009), along with 95% CIs (via 10 000 bootstrap replicates (Linkie & Ridout 2011)) using the overlap package in R (Meredith & Ridout 2014). We calculated overlap separately for each experimental site and then with data from both sites pooled. We considered there to be evidence of a change in temporal activity if overlap in activity distributions during control and human treatment was < 0.90.

Bobcats exhibited a consistent shift in temporal overlap between human and control treatments across both experimental sites (Table S2). We therefore quantified the degree to which this temporal shift constituted a reduction in diurnal activity in favour of nocturnality during the human treatment. For each bobcat detection on camera (n = 44 on 12 cameras), we calculated the absolute value of the difference (in hours) between the timestamp of the detection and the middle of the night (the midpoint between sunset and sunrise, averaged across the study period; 01:15) such that detections near midday received the highest values of this diurnal activity metric. We tested for the effects of playback treatment, experimental site and a treatment × site interaction on diurnal activity using LMM with camera site as a random effect.

Modelling medium-sized carnivore occupancy and detection frequency at camera sites

To test whether fear of humans affected medium-sized carnivore behaviour at the landscape scale, we developed a hierarchical model describing (1) use by a given species of individual camera sites within each experimental site and (2) frequency of detections of that species at used camera sites, a proxy for activity level. We based our model on multispecies occupancy models (Burton *et al*. 2012; Broms *et al*. 2016), but with two distinctions: (1) we consider camera site use (rather than occupancy *per se*), as individual carnivores could use more than one camera site, and (2) we modelled the frequency of detections of a given species at a camera site (a Poisson process), rather than the binary estimate of detected/not detected typically used in occupancy models. We treated each week of the experiment as a survey period (Wang *et al*. 2015; Moll *et al*. 2018), yielding five replicate surveys per treatment at each camera site. Three data points were excluded from the analysis when cameras failed to record data for the full week. We formulated our analysis as a zero-inflated negative binomial model (Moll *et al*. 2018), allowing occupancy at a camera site (binomial submodel) to vary between playback treatments, and explicitly modelling detection frequency (negative binomial submodel) as a function of experimental site, playback treatment and their interaction. We analysed the hierarchical detection frequency model in a Bayesian framework using the JAGS language (Plummer 2003) via the R2jags package (Su & Yajima 2015) in R. For a full model description and details on the Bayesian analysis (including JAGS code and model fit), see Appendices S1 and S2. Model results are present in Tables S3 and S4.

The above model indicated a substantial reduction in skunk detection frequency during the human treatment at both sites. To confirm the robustness of this result, we performed a simplified version of the analysis, using a Wilcoxon matched-pairs test to compare total skunk detections during the human and control treatments on each camera.

Medium-sized carnivore foraging trials

We created feeding patches (consisting of a single boiled chicken egg) at each of the 12 camera locations within each

experimental site. We estimated patch discovery rate (i.e. days required for a medium-sized carnivore to find and consume the egg, determined from camera trap images) as an index of carnivore foraging efficiency. Eggs were set out twice during each treatment period (during weeks 2 and 4), yielding a total of 96 trials. To standardise availability, we consider only those trials in which a medium-sized carnivore ultimately discovered the patch ($n = 36$), as some eggs were taken by other species (e.g. corvids) before being discovered by carnivores. Discovery rate data were log-transformed to satisfy normality assumptions and fit by LMM, using camera site as a random effect. We tested for effects of treatment, experimental site, species, session (first or second deployment during each treatment), and treatment × site interaction. Opossums made the majority of foraging patch discoveries ($n = 20$) and skunks made the remainder ($n = 16$), with no discoveries made by bobcats. We first analysed data from opossums and skunks combined, and then fit species-specific models, using the model terms just mentioned with the exception of species (Table S5).

Deer mouse spatial capture–recapture

We conducted a spatial capture–recapture study using four grids of live traps at each experimental site. Grids were trapped immediately prior to the start of any playbacks, and immediately following each playback treatment period. All captured mice were marked with unique ear tags. See Appendix S1 and Fig. S1 for live trapping details. We analysed live trapping data using spatial capture–recapture (SCR) models (Royle *et al*. 2013), which permit quantification of the amount of space used by individual animals (σ in SCR models; Appendix S1 and (Royle *et al*. 2013)). We modelled spatially explicit capture histories using a zero-inflated binomial model with data augmentation (Royle & Dorazio 2008; Royle *et al*. 2013). Detection probability and/or space use could be affected by playback treatment if mice alter their movements in response to treatment-induced changes in carnivore behaviour. We estimated the effect of playback treatment on detection probability and space use by calculating averages of these parameters (across all trapping grids) for trapping sessions following the control and human treatments. Treatment-level averages were then subtracted to estimate the average difference in parameter values between control and human treatments. If the 95% credible intervals (CrI) of the difference between treatments did not cross zero, we considered there to be evidence of a treatment effect on the parameter of interest (Table S6). Average values (± 95% CrI) of the space use parameter (σ) during each treatment were used to calculate the average area of habitat used during each treatment, following the procedure outlined by Royle *et al*. (2013, pg. 136). For a full description of the deer mouse SCR model and the Bayesian analysis of this model, see Appendices S1 and S2. Model results are presented in Tables S6 and S7.

Small mammal foraging trials

Two small mammal foraging patches, separated by < 3 m, were deployed at each of the 12 camera locations within each experimental site, one under protective cover (shrubs) and one in the open. Each patch consisted of an aluminium tray filled with 10 g of millet seed mixed into 1 l of sifted sand. Patches thus required time to exploit, allowing time for the accumulation of camera trap images and/or small mammal droppings in trays. Patches were deployed twice during each 5-week treatment period (during weeks 2 and 4) and were left in place for two consecutive nights, with millet and sand refreshed after the first night. We focus our analyses on the proportion of available patches visited on a given night and include only those trials in which visitation or lack thereof by small mammals (deer mice or woodrats) could be determined with high confidence based on the presence or absence of camera trap images and/or droppings ($n = 256$). Preliminary analysis indicated that open patches were largely avoided overall (Appendix S1, Table S8). We therefore restricted our analysis to patches under cover.

We coded whether a particular patch was visited (1) or not (0), and analysed these data using a generalised LMM with binomial error distribution, including camera site as a random effect. We tested for effects of treatment, experimental site, night (first or second night of patch deployment), moon illuminance and a treatment × experimental site interaction. Adequate model fit was assessed through inspection of scaled residuals using the DHARMa R package (Harting 2018).

RESULTS

Fear of humans drove significant changes in how mountain lions moved through the same physical landscape (Fig. 1). Mountain lions avoided areas of perceived human presence, encountering the playback grids 30% less often when human sounds were broadcast, and maintaining a 29% greater distance to the nearest speaker during human playbacks relative to controls (Figs. 2a and S2; LMM: Wald's $\chi^2_1 = 6.33$, $P = 0.012$). Mountain lions also moved more cautiously when hearing human playbacks, reducing average movement speed by 34% (Figs 2a and S2; LMM: Wald's $\chi^2_1 = 4.66$, $P = 0.031$).

Fear of humans had an overall suppressive effect on medium-sized carnivore behaviour (Fig. 2b). Bobcats reduced diurnal activity by 31% when hearing humans (Figs. 2b and S3; Table S2; LMM: Wald's $\chi^2_1 = 4.71$, $P = 0.030$), shifting their diel activity patterns towards increased nocturnality [overlap ($\hat{\Delta}$) in activity between treatment and control = 0.68 (95% CI: 0.48–0.86); Fig. S8]. Skunks were the only species to exhibit a reduction in overall activity (Table S4), reducing activity levels by 40% during the human treatment [Figs. 2b and S4; detection frequency model: treatment coefficient = −1.12 (95% CrI: −2.37 to −0.04)], and were therefore detected less frequently on camera traps (Wilcoxon test, $P = 0.007$; $n = 24$). When considering all trials in which a medium-sized carnivore discovered a provisioned food patch, fear of humans had a significant negative effect on food patch discovery rate (Table S5; LMM: Wald's $\chi^2_1 = 5.88$, $P = 0.015$). Species-specific models indicated that this effect was largely driven by opossums. The sound of humans led to a 66% reduction in opossum foraging efficiency (Figs. 2b and S5;

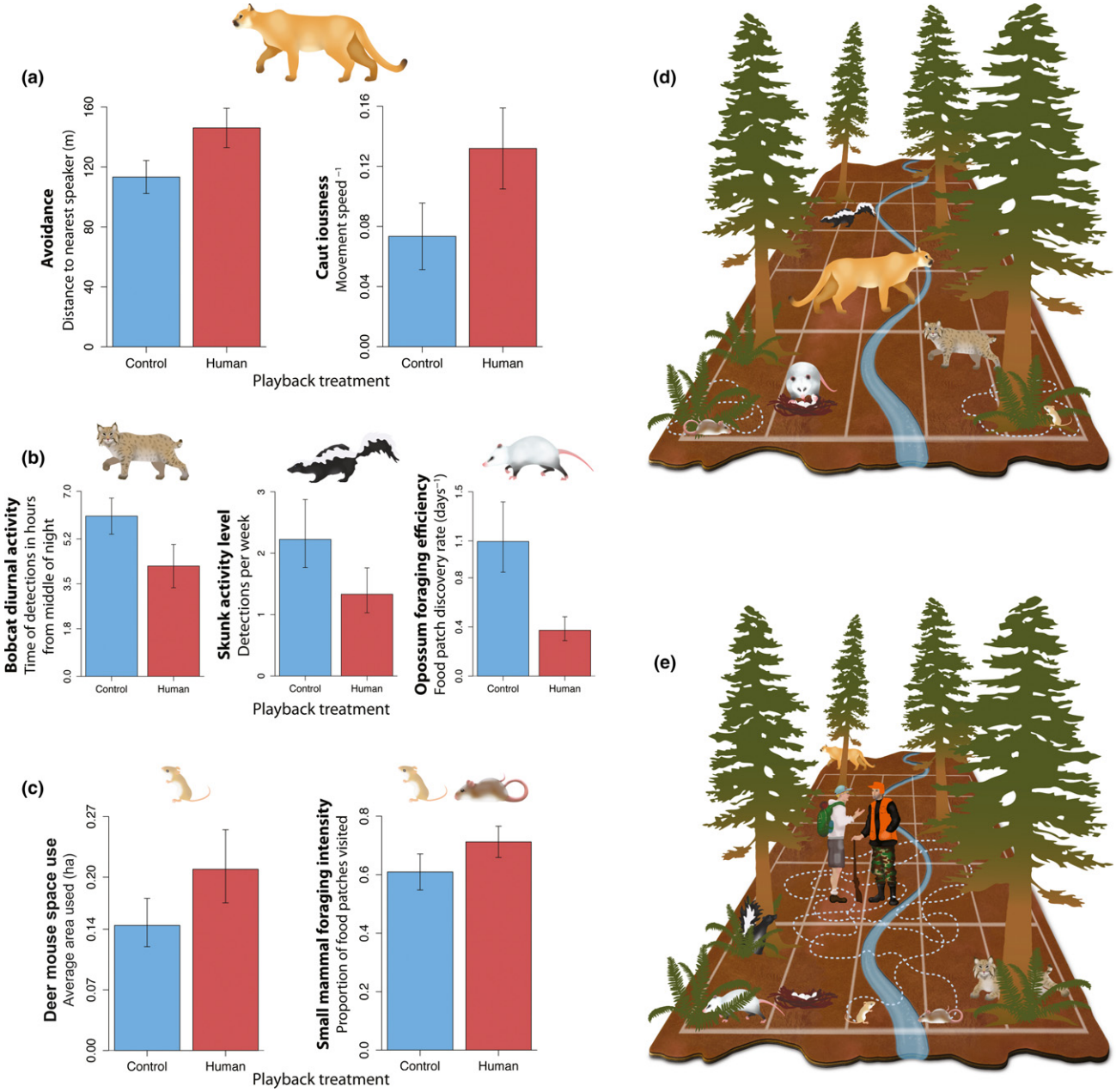

Figure 2 Fear of humans has landscape-scale impacts on wildlife across multiple trophic levels. (a) Fear of humans affects mountain movement behaviour. Mountain lion avoidance behaviour (left panel) is shown as average distance (m) to the nearest playback speaker and cautiousness (right panel) is shown as the inverse of average movement speed (mins/m). Bar plots illustrate means ± SEM. $N = 10$ control and 7 human. (b) Fear of humans suppresses medium-sized carnivore behaviour. Bobcat diurnal activity from camera trap detections (left panel; means ± SEM; $n = 26$ control and 18 human) is shown as time (h) from the middle of the night. Skunk overall activity level (middle panel) is shown as posterior mean and 95% credible intervals for number of detections per week on camera traps. Opossum foraging efficiency (right panel; means ± SEM; $n = 10$ control and 10 human) is shown as rate of discovery (days^{-1}) of provisioned food patches. (c) Suppression of larger predators induced by fear of humans benefits small mammals. Deer mouse space use (left panel) is shown as posterior mean and 95% credible intervals of average area (ha) used. Small mammal (deer mouse and woodrat) foraging intensity (right panel; mean ± SEM; $n = 64$ control and 73 human) is shown as proportion of provisioned food patches visited on a given night. All bar plots illustrate behaviours during control (blue) and human (red) playback treatments. (d) and (e) conceptual illustrations of the landscape-scale effects of fear of humans on wildlife communities. Where the human apex predator is absent or rare (d), large and medium-sized carnivores exhibit greater movement (mountain lion on grid), activity (bobcats and skunks active) and foraging (opossum eating a bird nest), while small mammals exhibit reduced space use (constricted movement paths, shown as dashed lines). Where humans are present (e), fear of humans suppresses the activity, foraging and/or habitat use of large and medium-sized carnivores, while small mammals increase their total space use and foraging intensity. Original artwork by Corlis Schneider.

Table S5; LMM: Wald's $\chi^2_1 = 8.77$, $P = 0.003$) such that opossums took on average 1.8 days longer to discover food patches during the human treatment.

Small mammals benefitted from the apparent presence of humans, increasing both the amount of habitat and number of foraging opportunities exploited. During the human

treatment, deer mice expanded their space use by 45% relative to controls (Figs. 2c and S6), increasing average area used by 649 m^2 (95% CrI = 116–1209 m^2) while maintaining an overall consistent detection probability across treatments (Tables S6 and S7). Mice and woodrats increased foraging intensity by 17% during the human treatment (Fig. 2c, Table S8; GLMM: Wald's $\chi^2_1 = 4.71$, $P = 0.030$), visiting a significantly higher proportion of provisioned food patches (Figs. S7 and S9).

DISCUSSION

Our results experimentally demonstrate that fear of humans as predators can have pervasive impacts across wildlife communities, suppressing movement and activity of large and medium-sized carnivores, with cascading benefits for small mammals (Fig. 2d and e). Thus, spatial variation in the perception of risk from an apex predator can itself create a landscape of fear (Gaynor *et al*. 2019), manifesting in widespread changes in wildlife behaviour.

Mountain lions significantly altered their movement through the same physical landscape in response to hearing humans (Fig. 1), exhibiting antipredator behaviours comparable to those previously documented in small-scale experiments (Smith *et al*. 2017), but at a substantially larger scale (Fig. 2a). Observational and manipulative studies have similarly found that risk from humans affects large carnivore behaviour across the landscape (Valeix *et al*. 2012; Ordiz *et al*. 2013b, 2019; Oriol-Cotterill *et al*. 2015; Suraci *et al*. 2019), including in our study area, where increased human development is correlated with impacts on mountain lion movement and habitat use (Wilmers *et al*. 2013; Wang *et al*. 2017). Our results confirm that, even in the absence of changes in human infrastructure (e.g. buildings, roads) or habitat fragmentation, increased human presence can impact large carnivore movement by inducing antipredator responses, which, if sustained for long periods, could lead to effective habitat loss for carnivores by limiting hunting and feeding behaviour (Smith *et al*. 2015) or forcing individuals to abandon high risk areas of their home range (Schuette *et al*. 2013).

Fear of humans had suppressive effects on medium-sized carnivore activity across all three study species (Fig. 2b), yet as expected from the diversity of carnivore behaviours, their exact responses differed. Our experimental results confirm previous correlational findings (Wang *et al*. 2015) that bobcats become more nocturnal in response to human presence, demonstrating that fear of humans may contribute to the documented global pattern of increased wildlife nocturnality in disturbed habitats (Gaynor *et al*. 2018). Fear of humans also impacts skunks and opossums, causing reductions in overall activity or foraging behaviour by these often human-associated species. These results highlight the trade-off such species face between the potential benefits of living in an anthropogenic environment [e.g. abundant food subsidies (Bateman & Fleming 2012; Newsome *et al*. 2015)] and the fear-induced costs of sharing habitat with humans (Fig. 2b). Interestingly, none of the three medium-sized carnivores exhibited changes in overall habitat use between treatments (number of camera sites used; Tables S3), potentially reflecting a limited capacity to do so, at least for species (i.e. skunks and opossums) whose relatively small home ranges likely overlapped substantially with our experimental sites (Appendix S1).

Finally, significant increases in small mammal space use and foraging documented during the human playback treatment (Fig. 2c) experimentally demonstrate that the suppression of carnivore behaviour induced by fear of an apex predator (in this case, humans) can have cascading effects on small mammal prey (Brook *et al*. 2012; Gordon *et al*. 2015). These cascading behavioural changes suggest that the presence of people may in some cases act as a 'human shield' (Berger 2007) for small mammals, reducing their perceived risk of predation from carnivores. Human shield effects have been suggested to occur in some large carnivore-ungulate systems, with ungulates preferring areas of high human activity because these areas are avoided by carnivores (Hebblewhite *et al*. 2005; Berger 2007; Muhly *et al*. 2011). If similar human shield effects for small mammals are common where human activity is high, this could ultimately lead to increased small mammal abundance in wildlife areas frequented by people, a potentially undesirable consequence of ecotourism (Geffroy *et al*. 2015).

Our work provides strong evidence that many of the globally observed changes in wildlife behaviour stemming from anthropogenic activity, including changes in large carnivore habitat use (Valeix *et al*. 2012), broader disruptions of animal movement (Tucker *et al*. 2018), and increased nocturnality (Gaynor *et al*. 2018), can be explained in part by the fear of humans as predators. Moreover, if fear of humans triggers substantial sublethal effects comparable to those fear itself has been demonstrated to cause in other predator–prey systems [e.g. increased physiological stress (Zanette *et al*. 2014), reduced reproductive success (Zanette *et al*. 2011; Cherry *et al*. 2016)], this may translate to additional widespread but largely unmeasured impacts of humans on wildlife populations. Given the potential for sublethal effects, apparently 'human-tolerant' species (e.g. medium-sized carnivores using developed areas) could nonetheless experience substantial costs from chronic exposure to perceived risk from humans (Clinchy *et al*. 2016). Pervasive fear of humans may also precipitate widespread community-level changes by disrupting natural predator–prey interactions. Human-induced antipredator behaviour could compromise top-down ecosystem regulation by large carnivores (Kuijper *et al*. 2016) and limit medium-sized carnivore suppression of small mammals (Levi *et al*. 2012). Given continued human encroachment into most wildlife habitats (Venter *et al*. 2016), we suggest that the fear we human 'super predators' inspire, independently of our numerous other impacts on the natural world, may contribute to widespread restructuring of wildlife communities.

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AUTHORSHIP

All authors conceived and designed the study. JPS led the fieldwork and analysis with support from CCW. JPS drafted the manuscript and all authors provided valuable feedback on the paper.

DATA AVAILABILITY STATEMENT

Data available from the Figshare Repository: https://doi.org/10.6084/m9.figshare.8315417

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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